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Scent marking in wild banded mongooses: 2. Intrasexual overmarking and competition between males

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Sexual selection has resulted in the elaboration of secondary sexual characteristics in many animals. Although mammalian scent glands, secretions and marking behaviour are commonly sexually dimorphic, these traits have received little attention compared to avian plumage and mammalian weaponry. Overmarking, when one individual places a scent mark directly over that of another individual, is of particular interest. Owing to the costs of repeatedly monitoring and covering the scent marks of rivals, overmarking may provide an honest indication of a male's resource-holding potential, perhaps explaining why female rodents exposed to experimental overmarks subsequently prefer to associate with males whose scent mark was on top. This study on wild banded mongooses, *Mungos mungo*, suggests that overmarking may primarily affect behavioural mating success through male competition not by female mate choice. First, chemical analyses of anal gland secretions demonstrated that males had individually distinctive scents, and a field experiment confirmed that mongooses were able to discriminate between scents from different individuals. Observations of overmarking patterns showed a relationship between overmarking score and behavioural mating success, but we found no evidence that females actively chose to mate with males with high overmarking scores. Instead, we found that males with higher overmarking scores first mate-guarded females at a significantly younger age than males with lower overmarking scores. Since mate-guarding males obtain the vast majority of matings, this suggests that overmarking may be an important component of intrasexual competition for mating opportunities in this species.

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In many birds, sexual selection has favoured extreme plumage elaboration (e.g. Indian peafowl, *Pavo cristatus*; Petrie et al. 1991), and because only high-quality males may be able to afford the production costs or handicap of carrying these elaborate ornaments, females may use these potential signals of quality in mate

choice (Zahavi 1975). In contrast, while most mammals lack elaborate visual ornaments, many have developed highly specialized scent glands (reviewed in Brown & Macdonald 1985). These glands, their secretions and associated marking behaviour are commonly sexually dimorphic, and are usually more developed in males, which has led to the suggestion that scents or scent-marking behaviour may be a mammalian equivalent of a peacock's tail (Penn & Potts 1998a). There is extensive evidence that scent marking is involved in intrasexual competition among males (reviewed in Ralls 1971; Johnson 1973; Gosling & McKay 1990), and it is generally recognized that most scent marking is related to the benefits of being chosen as a mate or controlling access to mating opportunities (Roberts 2007). However, little work on the detailed patterns of scent-marking behaviour and its role in sexual selection has been conducted.

For scents to be important in mate choice they must be costly and reliable signals of quality (Zahavi 1975). Although scent

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production costs are difficult to quantify (Penn & Potts 1998a), the cost of distributing scents throughout the environment is likely to be great, as regular scent marking potentially exposes individuals to increased predation risk (e.g. Viitala et al. 1995) and may even reduce the marker's growth rate and body size through energetic trade-off (Gosling et al. 2000). In addition to its potential effects on scent production and scent composition, sexual selection may therefore also shape the deposition or distribution patterns of scent marks.

Overmarking occurs when one individual deposits a scent mark directly on top of the scent mark of a conspecific (Johnston et al. 1994). As only high-quality individuals are likely to be capable of bearing the costs of consistently overmarking rivals, the relative position of scent marks may reflect the marker's resource-holding potential (see Rich & Hurst 1998, 1999; Gosling & Roberts 2001). Perception studies on laboratory rodents showed that investigators of overmarks not only 'knew' which scent was on top, but also preferred to associate with those individuals subsequently. When golden hamsters, *Mesocricetus auratus*, were presented with an experimental overmark, even one that was only partially overlapping, they subsequently showed evidence of having assigned greater significance to the top mark (Johnston et al. 1994, 1995). These females preferred to associate with top scent males in subsequent choice tests (Johnston et al. 1994, 1995; meadow vole, *Microtus pennsylvanicus*: Johnston et al. 1997), and captive pygmy lorises, *Nycticebus pygmaeus*, even preferentially mated with males to whose overmarks they had been experimentally exposed (Fisher et al. 2003). These results suggest that when a mark is deposited over an existing mark of another individual, subsequent investigators of the overmark can not only recognize which individual's mark is on top, but may also use this information when making mate choice decisions.

Banded mongooses overmark frequently, with over half of all observed scent marks at least partially overlapping an existing scent mark (Jordan et al. 2010). Members of each sex preferentially overmark the scents of same-sex individuals (Müller & Manser 2008a; Jordan et al. 2011), and previous work has shown that anal gland secretions (AGS) are sex-specific and that factors pertaining to the most recent mark influence the overmarking response of investigators (Jordan et al. 2011). Groups contain no clear dominant pair, instead comprising a core of breeding adult males (2–15 males/group), and multiple (1–8) breeding females (Rood 1975; Cant 2000; Cant et al. 2010). Males compete intensively with male relatives for mating opportunities with close female relatives during highly synchronous oestrous periods (Cant 2000). We investigated whether patterns of overmarking are related to mating success, defined here as the proportion of mating attempts that resulted in prolonged copulation, and to our knowledge this is the first study to do so in wild mammals. Specifically, we tested two hypotheses about the role of overmarking in mating competition. First, females might make mate choice decisions directly on the basis of overmarking scores ('female choice'). If so, we predict that males will overmark each other competitively, that is place their marks on top of those of other males, and females will preferentially mate with males with higher overmarking scores. Alternatively, males might use scent in competitive interactions with rivals, allowing them to monopolize access to females independent of female choice ('male competition'). In this case, we predict that males with higher overmarking scores will be more successful at monopolizing matings, but that females will exhibit no preference for such males in situations where they are able to exert mate choice. Additionally, we would also predict that mate-guards will be more likely than nonguards to have their scent mark on top at the end of scent-marking bouts. These hypotheses rely on the assumption that individuals

encountering scent marks are able to identify which individual deposited the scent mark. We tested this by assessing the individuality of male scents using chemical analyses, and by conducting a presentation experiment in the field to assess whether mongooses were able to discriminate between scents from different individuals. Finally, behavioural observations were conducted to determine whether overmarking score was related to mating success, and to assess the potential roles that overmarking may play in female choice or direct male–male competition.

METHODS

The general methods were identical to those described in the first paper in this series (Jordan et al. 2011) except for the following differences and additions.

Scent Collection and Composition Analysis

To determine whether males had individually distinctive scent profiles, 168 AGS samples (four samples per male) were collected from 42 males from six groups. The first and last samples from the same male were collected 287.1 ± 128.2 (mean \pm SD) days apart (range 84–445 days). Within the population, samples were collected from between seven and nine males from each of five groups, allowing separate statistical analyses for individuality to be conducted within social groups. During captures, individuals were weighed under anaesthesia using an electronic balance (Sartorius TE4101, Sartorius AG, Goettingen, Germany).

To account for the potential effects of weight and age (which correlate with each other), we estimated a condition index for adult males, which incorporates these two variables using the standardized residuals of a regression of body mass on age (with all adult males included in the regression).

Individual Discrimination Experiment

To determine whether mongooses could discriminate between scents from different mongooses, we conducted 15 trials of a field presentation experiment employing a habituation–dishabituation technique. First, we simultaneously captured two adult male littermates from the same social group, and collected four samples of AGS from each (for details of capture and collection procedure, see Jordan et al. 2010, 2011). In each trial, a target adult male recipient that was foraging naturally was approached and presented with four samples at 10 min intervals, and all samples within each trial were collected from adult males (>1 year). The first three samples ('A1', 'A2', 'A3') were from one individual, and the final sample ('B') was from a littermate of the first. If the individual discriminated between scents from the two individuals, and if scents from individuals are individually specific, then recipients would be expected to habituate to scents from the first individual (as they were all similar), before showing a heightened interest to the final sample presented as this was from the second individual. This paradigm has been successfully used previously to demonstrate that scents were individually specific, most notably in golden hamsters (Johnston 1993). Recipient responses to each sample were recorded using a tripod-mounted camcorder (JVC miniDV Digital Video Camera, model GR-D240EK), and investigation duration (the time the recipient spent with its nose within 1 cm of the sample) was measured to the closest frame (30 frames/s) using Panasonic MotionDV Studio after semiblind extraction (measurements were conducted by N.R.J. on randomly labelled clips 12 months later). After the recipient moved 1 m or more from the sample, further investigation bouts were not recorded. To ensure that samples were of the same effective age as each other at the

time of presentation, their removal from the freezer was staggered by 10 min, in line with the intended time between presentations in the field. Samples were transported to the field on ice, and, immediately prior to presentation, a small droplet (ca. 0.05 ml) of secretion was removed on the end of cleaned stainless steel forceps, and dropped on to a glass slide wrapped in cotton gauze.

Behavioural Observations

We conducted behavioural observations to determine whether overmarking frequency was related to mating success. We were primarily interested in whether females based mate choice decisions on male overmarking, or whether males used overmarking directly in male–male competition. We estimated each individual male's 'overmarking score' as the proportion of encountered adult male scent marks that each male overmarked. Scent marking and overmarking events were recorded by critical incident sampling (Altmann 1974), and overmarking was defined as the placement of a scent mark on an existing scent mark produced by another individual, so that the two scents were at least partially overlapping (*sensu* Johnston et al. 1994). When the first individual was seen to scent-mark a location, the scent mark type, the substrate marked and the identity of the individual that scent marked were recorded. Each location was given a unique identifying number (the 'scent station'), and all investigation (sniffing or licking) and overmarking by subsequent visitors to each scent station were recorded, in order, until the group moved away from the site. Responses were assessed only in relation to the most recent (or top) scent at a site, as previous analyses showed that this was more important than the original/bottom scent in determining the investigator's overmarking response (Jordan et al. 2011). Analyses only included adult males with five or more mating attempts and 10 or more encounters with scents made by other adult males, so that sufficient events were included to ensure accurate proportions were calculated.

During oestrous periods, some males act as 'mate-guards' by consistently following receptive females, staying within 2 m and aggressively attacking all other males that come within range (Cant 2000). Paternity analyses have shown that mate-guarding males account for over 80% of paternity (Nichols et al. 2010). Adult males that are unable to monopolize females in this way are 'nonguards'. Nonguards were all adult males not mate guarding during an oestrous session, and included 'pests' (Cant 2000), which tended to follow at a short distance, continually harassing mate-guards and attempting to copulate with the female. The period from the first to the last observed mating or mate guarding was termed 'group oestrus' (Cant 2000), and data were collected during 61 group oestrous periods in five groups (mean \pm SD = 12.2 \pm 3.03 per group, range 8–16). Estimates of mating success and male–male competition were recorded using a combination of continuous critical incident sampling and 20 min focal watches of females. During focal watches, the identity of the closest male and all males within 2 m were noted each minute, and all instances of mounting and mating were recorded on occurrence using a hand-held Psion II data logger (model LZ-64). A 'mating attempt' involved the male grabbing the female around the waist and attempting to climb onto her from the rear, and a mating attempt that was uninterrupted for 30 s or more was scored as a 'mating' (Cant 2000). Male 'mating success' was scored as the proportion of mating attempts that progressed to successful mating (i.e. continued for 30 s or more), excluding mating attempts involving primiparous females which did not produce pups in the resulting litter. The 'relative harassment' of each mate-guard by nonguards in each oestrous session was estimated as the mean number of nonguards within 2 m. Within each oestrous period, focal observations were conducted during the same observation session on two mate-guarding males.

Each of these 20 dyads contained a unique combination of males, and data were collected from four groups. Where more than two males were mate guarding, focal observations were conducted on the males with the highest and lowest overmarking scores, respectively.

Statistical Analyses

Scent mark composition

Chemical data were analysed following chemical and statistical methods described in detail in Jordan et al. (2011). Log-transformed percentage abundances were derived from absolute abundances of 35 discrete compounds, which were reduced and made independent by entering them into a principal components analysis (PCA). For all 42 males, a discriminant function analysis (DFA) was conducted by entering the seven principal components derived using the Kaiser method (Kaiser 1960) simultaneously. Post hoc 'bootstrapping' analyses were conducted in 'R' (R Development Core Team 2008) on the results of the DFA. This allowed us to determine the probability that a cross-validated correct assignment value was achieved by chance, and we followed the methods of Müller & Manser (2008b).

Individual discrimination experiment

A repeated measures one-way ANOVA was used to test for differences between the four AGS samples and a planned post hoc least-square difference (LSD) pairwise test was conducted to test for habituation (sample A1 versus A3) and dishabituation (A3 versus B) only.

Behavioural observations

Behavioural data were analysed using Genstat Release 10.1 (Lawes Agricultural Trust, Rothamsted, U.K.).

Intrasexual overmarking. To investigate factors affecting the probability that an encountered scent mark previously deposited by an adult male would be overmarked, we constructed binomial generalized linear mixed models (GLMMs) with a logit-link function, and fitted overmarking response as the response variable (1 = overmarked, 0 = not overmarked), with a binomial total of 1. Analyses were conducted on encounters by 82 adult males with 2257 scent marks deposited by 82 adult males at 989 unique scent stations in six groups. Group identity, Investigator ID, Previous marker ID and unique mark site were included as random terms.

Mating success. To investigate the factors affecting the probability that a mount by an adult male on an adult female would result in a successful mating (lasting >30 s), data were fitted to a binomial distribution with a logit-link function and binary response terms (1 or 0) indicating whether or not successful mating ensued. Separate GLMMs were conducted on (1) all males, before (2) mate-guards and (3) nonguards. (Sample sizes are presented in the Results) In all three models, group identity, oestrous period, male ID and female ID were included as random terms.

RESULTS

Scent Mark Composition

The seven principal components explained 72.6% of the original variance. The corresponding DFA assigned 6.0% of the cross-validated samples to the correct individual, which is significantly higher than the 2.4% expected by chance (Table 1). As individual discrimination is likely to be most important within social groups, we conducted DFAs for males within each group separately. In three

Table 1
Summary of discriminant function analyses (DFA) for all males in the population and males from five social groups independently, showing the significance of post hoc bootstrapping analyses on the percentage correct assignment

Individuals in analysis	N (males)	N (samples/male)	PCs/% variance explained	% Assignment expected by chance	% Correct assignment (cross-validated)	P (bootstrapping)
All males	42	4	7/72.6	2.4	6.0	<0.0001
Group B males	9	4	9/82.6	11.1	36.1	<0.0001
Group D males	9	4	8/82.1	11.1	48.6	<0.0001
Group F males	8	4	8/84.2	12.5	18.8	0.189
Group H males	7	4	7/84.4	14.3	0.0	N/A
Group V males	7	4	7/85.0	14.3	37.0	0.033

The number of principal components (PCs) entered into the DFA, and the percentage variance they encapsulate from 35 detected compounds in the raw secretions are also shown.

of five groups, the corresponding DFAs assigned a significantly greater percentage of the cross-validated samples to the correct individual than would be expected by chance (Table 1). Figure 1 shows chromatograms for two adult males, with each male sampled twice for comparison.

Individual Discrimination Experiment

The repeated measures ANOVA showed that individuals responded differently to the four AGS samples ($F_{3,42} = 2.953$, $P = 0.043$; Fig. 2). Mongooses habituated to the repeated presentation of scent from one individual (mongooses spent significantly less time investigating the third sample [A3] versus the first sample [A1] from the same individual; $P = 0.003$). On introduction of the scent of a second individual (sample B), mongooses spent significantly longer investigating it than they did the last sample (A3) from the first male ($P = 0.033$).

Behavioural Observations

Marking, mating and condition

Of 465 observed mating attempts involving multiparous adult females, 167 resulted in successful mating (39.9%), and overmarking score was weakly positively correlated with mating success in adult males ($r^2 = 0.16$, $N = 32$, $P = 0.025$; Fig. 3). The two main ways in which male intrasexual overmarking score might be related to mating success are by female choice and male–male competition for access to females, both of which predict a relationship between male ‘quality’ and overmarking score. We found

that the probability of a male overmarking an encountered male scent mark was related to both the estimated condition and the age of the investigating male relative to the male whose scent it encountered (Table 2). Males of the same age as the previous scent marker were less likely to overmark the scent if they were in better condition, but younger males increased their overmarking response to scents if they were in good condition (Fig. 4). Neither relative dominance (measured as the proportion of oestrous sessions spent mate guarding) nor group oestrous state affected overmarking likelihood (Table 2), but mate-guards were more likely to have their scent mark on top of a scent station at the end of scent-marking bouts than were nonguards ($\chi^2_1 = 186.2$, $P < 0.001$).

Female choice

To determine whether female mate choice was related to male intrasexual overmarking score, we first looked for evidence of female choice in general, before investigating female choice in situations where they were able to choose. The GLMMs assessing factors affecting the likelihood that an attempted mating would reach completion showed that female age was an important determinant of mating success (Tables 3–5). Mountings were more likely to progress to successful mating with younger females, suggesting that older females might be more selective about which males they completed matings with. However, we found no evidence that male intrasexual overmarking score affected the likelihood of mating success in any context (Tables 3–5).

Although mate-guards were more likely to mate with the female they were mate guarding, we observed 67.7% (21/32) of mate-guarded females mate at least once with a male who was not their

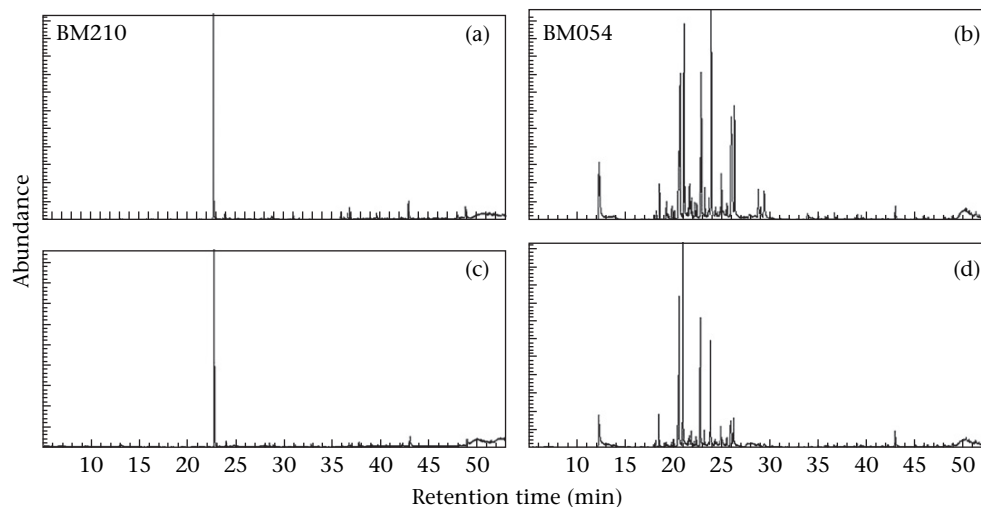


Figure 1. GCMS profiles for anal gland secretions from two adult males (BM210 [a, c] and BM054 [b, d]) from the same social group. Samples were taken in (a, b) January 2006 and (c, d) June 2006. In each chromatogram, retention time (min) is plotted against abundance (on an arbitrary scale), with each spike representing a particular chemical compound.

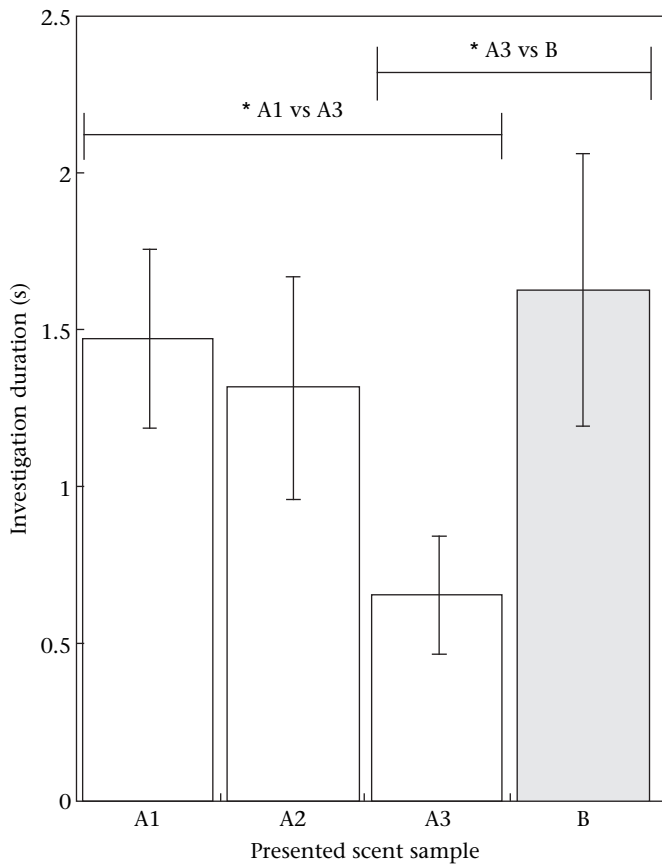


Figure 2. Mean \pm SE number of seconds individuals spent investigating anal gland secretion samples from two adult male littermates from the same group as the recipient. During habituation trials, three samples from one male were presented in sequence (A1–A3), before the sample of a second male was presented during test trial B. $N = 15$ trials in six groups. $*P < 0.05$.

current mate-guard. These females usually did so away from the main group and the mate-guard male in particular. It does not appear that females chose to mate with males on the basis of their intrasexual overmarking score as these mated nonguards had similar intrasexual overmarking scores to ‘cuckolded’ mate-guards

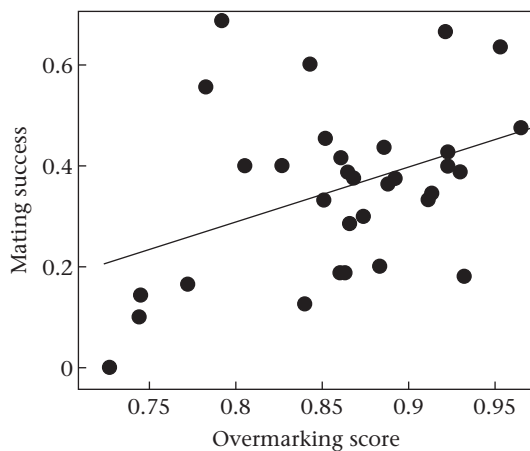


Figure 3. The correlation between male overmarking score (proportion of encountered male scents that were overmarked) and male mating success (proportion of attempted mountings of multiparous adult females that continued for 30 s or more). Each of the 32 points represents a single adult male.

Table 2

GLMM on factors affecting the probability that an encountered scent mark previously deposited by an adult male would be overmarked

	Wald statistic (χ^2)	df	P
Full model			
Relative age	11.03	2	0.004
Condition	0.85	1	0.356
Relative dominance	2.18	1	0.336
Group oestrous state	0.03	1	0.863
Relative age*condition	6.61	2	0.037
Minimal model			
	Category	Coefficient estimate	SE
Constant		2.096	0.138
Relative age	Older	0.000	0.000
	Same	0.202	0.198
	Younger	−0.384	0.198
Relative age*condition	Older	0.000	0.000
	Same	−0.213	0.196
	Younger	0.288	0.196

Coefficient estimates represent the change in the dependent variable relative to the baseline category and can thus be interpreted as measures of effect size. Group identity (estimated variance component = 0.022, SE = 0.042), Investigator ID (estimated variance component = 0.039, SE = 0.054), Previous marker ID (estimated variance component = 0.00, SE = bound) and unique mark site (estimated variance component = 1.156, SE = 0.215) were included as random terms. Relative age is the age of the investigator of the scent relative to the male that deposited the encountered scent. Condition scores were standardized residuals obtained by regressing male weight on age. Relative dominance is the proportion of oestrous sessions that the investigator of the scent spent mate guarding relative to the male that deposited the encountered scent.

(paired t test: $t_{33} = -0.42$, $N = 34$, $P = 0.680$). In fact, most of these nonguards had lower intrasexual overmarking scores than the mate-guard whose female they successfully mated with.

Male–male competition

As males currently mate guarding a female were more likely to complete matings successfully with that female than were other males that mounted her (Table 3), we looked at the relationship between overmarking and male–male competition for mate-guard status. The age at which males were first able to mate-guard a female successfully was related to their intrasexual overmarking score. In 10 pairs of littermates with significantly different intrasexual overmarking scores (paired t test: $t_9 = 4.11$, $N = 10$, $P = 0.003$), the male with the highest intrasexual overmarking score first mate-guarded a female significantly earlier (87.6 ± 32.9 days earlier) than the male with the lowest (paired t test $t_9 = -2.66$, $N = 10$, $P = 0.026$; Fig. 5a). This is despite no significant difference between the males in mean weight (during the month the first time one of the males guarded

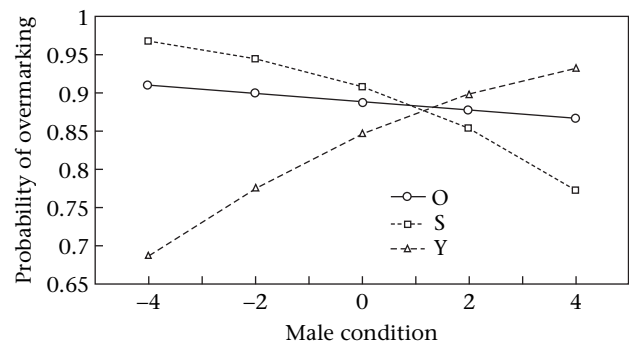


Figure 4. The effects of male condition and relative age on the probability of overmarking an encountered male scent. Condition was estimated as the residuals of body mass on age, and relative age refers to the age of the individual relative to the previous marker (O = older, Y = younger, S = same). Line shows predicted means from a GLMM, controlling for other significant terms in the model.

Table 3

GLMMs on factors affecting the probability that a mount by an adult male on an adult female would result in a successful mating (lasting >30 s): all males

	Wald statistic (χ^2)	df	P
Full model			
Mate-guard status	11.68	1	<0.001
Female age	5.17	1	0.023
Male overmarking score	0.93	1	0.335
Male age	0.90	1	0.344
Female status	0.75	1	0.388
Male condition	0.42	1	0.516
Minimal model			
	Category	Coefficient estimate	SE
Constant		-0.745	0.194
Mate-guard status	No	0.000	0.000
	Yes	0.724	0.212
Female age		-0.541 ⁻³	0.238 ⁻³

Data were fitted to a binomial distribution with a logit-link function and binary response terms (1 or 0) indicating whether or not successful mating ensued. Condition scores were standardized residuals obtained by regressing male weight on age. Analysis was conducted on 486 mounts by 43 males on 34 females during 45 group oestrous periods in six groups. Group identity (estimated variance component = 0.00, SE = bound), oestrous period (estimated variance component = 0.431, SE = 0.221), male ID (estimated variance component = 0.016, SE = 0.103) and female ID (estimated variance component = 0.030, SE = 0.094) were included as random terms.

a female; paired *t* test: $t_9 = -0.65$, $N = 10$, $P = 0.535$). Additionally, males with higher intrasexual overmarking score than a fellow mate-guarding male in the same session (paired *t* test: $t_{18} = -5.76$, $N = 19$, $P < 0.001$) suffered less encroachment by other males to within 2 m of their mate-guarded female (paired *t* test: $t_{18} = 2.56$, $N = 19$, $P = 0.020$; Fig. 5b). Females that were mate-guarded by males with higher intrasexual overmarking scores tended to be older (paired *t* test: $t_{18} = -1.98$, $N = 19$, $P = 0.063$), and heavier (paired *t* test: $t_{14} = -2.03$, $N = 15$, $P = 0.062$). Males with higher intrasexual overmarking scores were also heavier than males with lower intrasexual overmarking scores (paired *t* test: $t_{18} = -2.32$, $N = 19$, $P = 0.032$), despite being of a similar age (paired *t* test: $t_{17} = -0.60$, $N = 19$, $P = 0.554$).

DISCUSSION

To assess the potential role of male overmarking behaviour on mating success, we investigated the information content and perception of scents, and natural patterns of overmarking and mating in wild banded mongooses. Chemical analyses of scents indicated that male banded mongooses have a degree of individual

Table 4

GLMMs on factors affecting the probability that a mount by an adult male on an adult female would result in a successful mating (lasting >30 s): mate-guards only

	Wald statistic (χ^2)	df	P
Full model			
Female age	5.58	1	0.020
Male age	1.86	1	0.173
Female status	1	1	0.319
Male overmarking score	0.05	1	0.830
Male condition	0.02	1	0.883
Minimal model			
	Coefficient estimate	SE	
Constant	-0.175	0.143	
Female age	-0.635 ⁻³	0.269 ⁻³	

Data were fitted to a binomial distribution with a logit-link function and binary response terms (1 or 0) indicating whether or not successful mating ensued. Condition scores were standardized residuals obtained by regressing male weight on age. Analysis was conducted on 251 mounts by 38 males on 32 females during 35 group oestrous periods in six groups. Group identity (estimated variance component = 0.00, SE = bound), oestrous period (estimated variance component = 0.036, SE = 0.152), male ID (estimated variance component = 0.030, SE = 0.132) and female ID (estimated variance component = 0.00, SE = bound) were included as random terms.

Table 5

GLMMs on factors affecting the probability that a mount by an adult male on an adult female would result in a successful mating (lasting >30 s): nonguards only

	Wald statistic (χ^2)	df	P
Full model			
Male overmarking score	2.44	1	0.128
Male age	1.46	1	0.232
Female age	1.33	1	0.250
Male condition	0.40	1	0.531
Female status	0.27	1	0.606
Female age*male condition	5.75	1	0.017
Minimal model			
	Coefficient estimate	SE	
Constant	-0.888	0.258	
Female age*male condition	-0.125 ⁻²	0.522 ⁻³	

Data were fitted to a binomial distribution with a logit-link function and binary response terms (1 or 0) indicating whether or not successful mating ensued. Condition scores were standardized residuals obtained by regressing male weight on age. Analysis was conducted on 235 mounts by 40 males on 29 females during 39 group oestrous periods in five groups. Group identity (estimated variance component = 0.00, SE = bound), oestrous period (estimated variance component = 0.664, SE = 0.425), male ID (estimated variance component = 0.244, SE = 0.318) and female ID (estimated variance component = 0.00, SE = bound) were included as random terms.

specificity in anal gland secretions, and field experiments showed that mongooses can discriminate between scents from different individuals. Behavioural observations of overmarking within adult males suggest a relationship between male condition, intrasexual overmarking score and mating success. However, although male intrasexual overmarking score was positively correlated with mating success, overmarking did not seem to affect mating success via female mate choice. Where females appeared to exert a degree of choice in their mating partner, by temporarily leaving their mate-guard to mate with another male, they did so to mate nonguards with similar intrasexual overmarking scores to their current mate-guard. As mate-guards account for over 80% of matings (Cant 2000) and obtain over 80% of paternity (Nichols et al. 2010), we investigated the relationship between overmarking and acquisition of mate-guard status. In paired littermates, males with higher intrasexual overmarking scores first mate-guarded a female at a significantly younger age than paired males, despite no significant difference in weight between these males, and these males suffered less encroachment by other males around the female they were guarding. These results suggest that overmarking in mongooses is not involved in female choice, but instead may form the basis upon which males assess their relative competitive ability and decide whether or not to mount a physical challenge (Roberts 2007).

Although only a relatively low percentage of scents were correctly assigned to individuals, this may in part be a result of the large number of males (42) included in the analysis, as scents were assigned to the correct individual significantly more often than expected by chance. Additionally, and in contrast to many other studies (but see Buesching et al. 2002a, b), we were able to sample the same individuals repeatedly over an extended period (2 years), and our findings suggest that the scents of individual males were relatively stable over this period. As individual signatures must only remain consistent or recognizable for long enough that recipients may update their templates (Dale et al. 2001), and given that scent marks are encountered frequently by others within the group, significant correct assignment of scents that were collected such a long time apart is perhaps surprising. Additionally, as Müller & Manser (2008b) pointed out in their study of mongoose vocal recognition, it is probable that our analyses may not have measured some parameters relevant for individual discrimination of these scents. Whereas highly individualized signals do not necessarily imply the presence of individual recognition or discrimination (e.g. McCulloch et al. 1999), our results also indicate that low assignment

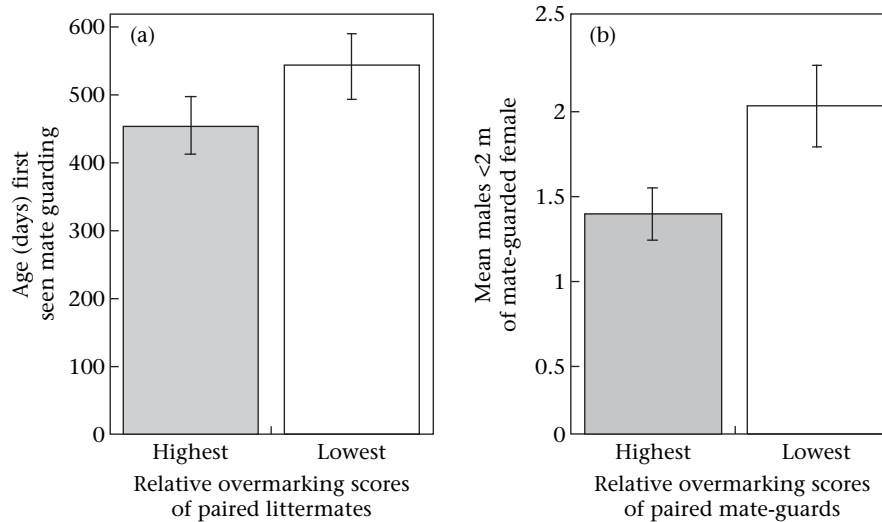


Figure 5. (a) The mean age \pm SE at which male littermates with significantly different intrasexual overmarking scores were first seen to mate-guard females. (b) The mean number \pm SE of nonguard males within 2 m of females that were guarded in the same session by males with different relative intrasexual overmarking scores.

rates of single signals to the correct individual in DFAs need to be interpreted cautiously, and may not necessarily imply absence of individually specific information and individual discrimination.

That mongoose scents are individually specific is further supported by our field experiment. Following habituation to anal gland secretions presented sequentially from a donor male, recipients displayed renewed responsiveness to a scent collected from a male littermate of this donor male. This suggests that scents from adult male littermates were individually specific, and that recipients were able to discriminate between these scents. The various difficulties of sequentially presenting individual wild mongooses with multiple scent stimuli under comparable conditions forced us to use a rather less robust alternative than the habituation recovery protocol used in other studies (Evans 1997; Blumstein & Daniel 2004), and we were not able to conduct parallel tests to control for the possibility that subjects may have dishabituated even to control tests (see Penn & Potts 1998b). Nevertheless, our habituation–dishabituation paradigm adds support to statistical classification of chemical differences in scent from individual males, suggesting not only that scents are individually specific but also that mongooses can discriminate between the scents from different individuals.

Although intrasexual overmarking score was positively correlated with behavioural mating success in male banded mongooses, we found no evidence for direct female choice of males on the basis of intrasexual overmarking score. When females ‘escaped’ their mate-guard to mate with nonguards (and so were able to exercise choice), they did not choose to mate on the basis of the male’s intrasexual overmarking score. This result is similar to that for prairie voles, *Microtus ochrogaster*, which did not choose mates on the basis of the frequency or placement of male scent marks which were manipulated experimentally (Thomas 2002). In contrast to banded mongooses, however, male prairie voles do not seem to engage in male–male overmarking (Thomas & Kaczmarek 2002). In contrast to overmarking scores, mate-guard status in our study seemed to be the strongest determinant of mating success, with successful mating more likely to involve mate-guards than nonguards. Indeed, intrasexual overmarking score fell out of all models investigating factors affecting mating success. While the majority of matings occurred with males with higher intrasexual overmarking scores (their mate-guards), it was not possible to describe this as active mate choice of one particular characteristic (intrasexual

overmarking score), as these males also tended to be older and heavier.

An alternative explanation of the relationship between male intrasexual overmarking score and mating success is that male overmarking patterns may be involved in male–male competition, with mating attempts potentially failing because of male–male interference, rather than by female choice. Our results supported this hypothesis. Males with high intrasexual overmarking scores mate-guarded females earlier and suffered less harassment than males with low intrasexual overmarking scores. Nonguards appeared to direct their attention to oestrous females mate-guarded by males with low intrasexual overmarking scores, and in doing so may avoid conflict with males with high intrasexual overmarking scores. As previous work suggests that heavy females are more likely to conceive (Hodge 2003; but see Cant 2000), and older females produce more pups (Cant 2000), it is likely that males with high intrasexual overmarking scores obtain a greater share of the most productive matings in the group. This is because males with high intrasexual overmarking scores tended to mate-guard females that were significantly older and heavier than those mate-guarded by males with lower intrasexual overmarking scores. Unfortunately, however, the relationship between behavioural mating success and actual (genetic) male reproductive success is not yet known in this species.

The relative weight of males, corrected for age, also had an effect on their overmarking response. Although when individuals were older than the most recent marker, condition (age-corrected weight) had no significant effect on overmarking, when individuals were younger than the previous marker the probability of them overmarking a scent was affected by their condition. Individuals that were relatively heavy for their age were more likely to overmark older males than those that were relatively light for their age, perhaps because young heavy males are in a good position to compete with older males. Female meadow voles that ‘lost’ a staged dyadic encounter subsequently overmarked female conspecifics less than winning females did (Ferkin 2007). It is possible that, in banded mongooses and meadow voles alike, overmarking fewer scent marks of winners/more dominant individuals may reduce the chances of them being physically aggressive, which may be beneficial to both winners and losers because of the high costs associated with fighting (Gosling & McKay 1990; Ferkin 2007). However, we found that when the investigator and the most recent marker

were of the same age (i.e. littermates), individuals were less likely to overmark scents as their own condition increased, which perhaps reflects the lack of a need to assert themselves in this way because of their large size.

In summary, although intrasexual overmarking score was correlated with mating success in male mongooses, we found no evidence of female choice on the basis of male intrasexual overmarking score. Instead, our results suggest that intrasexual overmarking in male mongooses may form the basis upon which potential combatants assess their relative competitive ability and decide whether or not to mount a physical challenge. In this respect, overmarking may serve as an honest indicator of quality and dominance, and thus may play a similar role in mating competition to a badge of status (e.g. house sparrow, *Passer domesticus*, bib size, Nakagawa et al. 2007). Currently, it is not possible to state definitively whether males achieve higher mating success as a result of their higher intrasexual overmarking scores, or whether mate-guarding status results in higher intrasexual overmarking scores. Further studies on a variety of species in the natural environment are required to validate and build on laboratory studies, and are most likely to expand our understanding of the function and diversity of overmarking strategies.

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